Pre-Columbian agricultural landscapes, ecosystem engineers, and self-organized patchiness in Amazonia

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The scale and nature of pre-Columbian human impacts in Amazonia are currently hotly debated. Whereas pre-Columbian people dramatically changed the distribution and abundance of species and habitats in some parts of Amazonia, their impact in other parts is less clear. Pioneer research asked whether their effects reached even further, changing how ecosystems function, but few in-depth studies have examined mechanisms underpinning the resilience of these modifications. Combining archeology, archeobotany, paleoecology, soil science, ecology, and aerial imagery, we show that pre-Columbian farmers of the Guianas coast constructed large raised-field complexes, growing on them crops including maize, manioc, and squash. Farmers created physical and biogeochemical heterogeneity in flat, marshy environments by constructing raised fields. When these fields were later abandoned, the mosaic of well-drained islands in the flooded matrix set in motion self-organizing processes driven by ecosystem engineers (ants, termites, earthworms, and woody plants) that occur preferentially on abandoned raised fields. Today, feedbacks generated by these ecosystem engineers maintain the human-initiated concentration of resources in these structures. Engineer organisms transport materials to abandoned raised fields and modify the structure and composition of their soils, reducing erodibility. The profound alteration of ecosystem functioning in these landscapes coconstructed by humans and nature has important implications for understanding Amazonian history and biodiversity. Furthermore, these landscapes show how sustainability of food-production systems can be enhanced by engineering into them fallows that maintain ecosystem services and biodiversity. Like anthropogenic dark earths in forested Amazonia, these self-organizing ecosystems illustrate the ecological complexity of the legacy of pre-Columbian land use.

French Guiana | historical ecology | land-use legacy | raised-field agriculture | coupled human and natural systems

Some tropical landscapes long considered “pristine” are now known to have been densely occupied by humans in the past (1, 2), inspiring optimism that these environments and their biodiversity may be more resilient to intensive human use than often feared (3, 4). Among the most extensive apparently pristine landscapes are the forests and, by extension, the savannas of Amazonia. The extent to which Amazonian ecosystems were affected by pre-Columbian human activities is currently hotly debated. This controversy has bearing on much broader debates about how to conceptualize the history of forested and other tropical systems and the ecological footprint of past agriculture upon them (2, 5) and how to plan for the transition of these systems toward future global food, energy, and carbon needs (6–10). It still is argued whether the influence of pre-Columbian humans was minor and localized (11) or important and widespread (12, 13). The nature of this impact is also unclear. In addition to altering the species composition of communities and the distribution and frequency of different kinds of habitats, did pre-Columbian inhabitants also profoundly change ecosystem functioning (14, 15)?

We examine the impact of pre-Columbian farmers in seasonally flooded savannas in French Guiana. In this region, vegetation is a mosaic of interdigitated rainforest and edaphic savannas; many of the latter are seasonally flooded. As is becoming increasingly documented in several regions within the Neotropical lowlands (5), farmers constructed raised fields (a subset of wetland fields (5, 16]) and other earthworks in these environments. Part of the controversy about the extent of human modification of these landscapes centers around distinguishing which elevated structures are cultural features (raised fields and other earthworks) and which are natural features such as termite mounds (11, 17). How structures may be affected by interactions between cultural and natural processes has been largely ignored. In contrast to studies of the anthropogenic soils of forested Amazonia (e.g., ref. 18), few studies of raised fields in savanna environments (but see refs. 19 and 20 for outstanding examples) have integrated work in the range of disciplines necessary to tackle the complexity of coupled human–environment interactions (21) such as legacies of past land use (e.g., ref. 22). Important driving mechanisms thus may have been neglected. We focus on three questions: First, did past human modification of landscapes change how these ecosystems functioned? Second, did these changes increase the resilience of raised-field agroecosystems? Third, were these changes durable, and can they explain how the material signatures of long-abandoned raised-field landscapes have persisted to the present day? To address these challenging questions, we combined archeology, paleoecology, and aerial imagery to examine the scale of landscape modification by pre-Columbian people (Fig. 1 and SI 1 A–D) in a kind of environment that often has been considered marginal for agriculture (23). We used archeobotanical methods to study what crops people grew and integrated data from soil science and ecology to examine how these agricultural landscapes were constructed, how their soils were managed, and how past human actions continue to affect ecosystem functioning.

During the Late Holocene, pre-Columbian societies in many parts of lowland South America began to transform landscapes at a scale not seen previously (24). Dark-earth soils associated with intensive agriculture appeared in diverse sites in Amazonia and its periphery (5, 18, 25), and farmers constructed raised...
fields to provide crops with well-drained soils in seasonally flooded savannas (5, 26, 27).

Our research shows that, as in other parts of South and Central America that are considered unsuitable for agriculture today (5), pre-Columbian farmers constructed thousands of raised fields in the seasonally flooded coastal savannas of the Guianas (27, 28). They built conspicuous earthworks, including raised fields, canals, and ponds, that enabled them to practice intensive permanent (or semipermanent) agriculture in this low-lying region with highly seasonal rainfall [2.5–4 m, most of it during a December to July rainy season (29)]. In savannas along the Guianas coast, these “fossil” agricultural landscapes, long abandoned and their origin forgotten, are spread over ca. 600 km, from the Berbice River in Guyana to near Cayenne (Fig. S1E). They occur in basins of the Demerara Formation that are bounded by Late Quaternary marine terraces (30); they exhibit great diversity in size, shape, orientation, and location in the landscape (28) (Figs. S1 A–D and S2). They are difficult to confuse with small areas of raised beds constructed by Creole farmers after European colonization, which differ in form from those made by pre-Columbian inhabitants and occur mostly in previously forested habitats. Today, in what may represent an African tradition (31), Saramaka and Haitian immigrants continue to build and to farm localized patches of raised fields in savannas.

In savanna habitats, where waterlogged soils and parched, fire-prone vegetation alternate seasonally, pre-Columbian raised fields created new microenvironments where crops could grow. How did these new environments function when raised-field landscapes were abandoned several centuries ago? We hypothesize that the coupling of ancient actions of human engineers and the continued actions of other ecosystem engineers (32) caused a durable transformation of ecosystem functioning, generating feedbacks that drive self-organized maintenance of abandoned raised fields. In the following sections, we provide and analyze data on human modification and agricultural use of Amazonian landscapes. We show how feedbacks driven by ecosystem engineers maintain these modified landscapes and illustrate how analysis of self-organization can help us interpret the archeological record, as modified by postabandonment ecological processes.

Results and Discussion

Raised-Field Construction and Diversity in French Guiana. Raised fields of French Guiana show considerable variation in size and shape among sites. They include large round raised fields up to 5 m diameter, elongate ridges 1–4 m wide and usually 20–30 m (up to 140 m) long, and small, round structures ca. 1–1.5 m diameter. Our analyses show that pre-Columbian raised fields were constructed in a highly organized fashion, likely reflecting how pre-Columbian farmers managed water under differing drainage conditions. For example, in the K-VIII site near Kourou (Fig. S2), large square or round raised fields are located in sectors most subjected to prolonged flooding. In turn, elongate ridges are oriented along the slight slope, suggesting this configuration was designed to facilitate drainage. Upslope from these fields, in the best-drained parts of the complex, farmers created fields parallel to elevation contours, an orientation favoring water retention. All these types are known from other Neotropical raised-field sites (5). As in locations with other types of raised fields, sites with only small, round raised fields are regularly organized, often in a square-grid arrangement (Fig. 1). Whereas regular spacing of patches is common in self-organized landscapes of natural origins (33, 34), such symmetry in their orientation is quite unusual in flat landscapes lacking marked extrinsic environmental gradients (34).

The chronology of these ancient raised fields is best approached through a consideration of associated archeological remains. The newly excavated residential site Sable Blanc dates between 825 and 990 14C y B.P. (708–938 Cal y B.P.) (Table S1). These dates and analysis of ceramic styles link this site to the Barbacoeba culture, part of the Arauquinoid cultural tradition. Stratigraphy and stylistic analysis of ceramics shows the presence of a Barbacoeba occupation layer beneath a layer of the younger Thémire culture, also part of the Arauquinoid tradition, in the Bois Diable site (Table S1 and SI Text). The Arauquinoid tradition originated in the Middle Orinoco around 1,500 y B.P. (35), reached western coastal Suriname around 1,300 y B.P., and then spread eastward to near present-day Cayenne (36). In French Guiana, the Barbacoeba and Thémire cultures flourished between ca. 1,000 and 800 y B.P. and 800 and 500 y B.P., respectively. Barbacoeba and Thémire habitation sites are located in the higher (never flooded) marine terraces parallel to the coast, and their ceramics are characterized by bowls, jars, and griddles. Diagnostic decoration includes zoomorphic and anthropomorphic adornos, in particular stylized twin adornos (36).

New dates from organic matter of the uppermost sector of buried A horizons (Fig. 2) beneath raised fields at the Bois Diable and K-VIII sites date to 750 ± 40 14C y B.P. (670–700 Cal y B.P.) and 1,010 ± 40 14C y B.P. (920–950 Cal y B.P.), respectively, showing that the occupation of Barbacoeba residential sites was broadly contemporaneous with raised-field construction (Table S1). The people of this tradition thus appear to be those responsible for the massive late Holocene human-driven transformation of coastal Guianan landscapes. A wooden shovel found in western Suriname, dated to 790 ± 30 14C y B.P. (693–733 Cal y B.P.) (37), is the only preserved example of the kinds of tools these people used to construct earthworks.*

Study of these buried soil surfaces in pre-Columbian raised fields gave insight into their construction and how soils were managed. The buried A horizon observed in large raised fields in the K-VIII and Bois Diable sites was at about the same level as the surrounding matrix (Fig. 2). On top of the buried A horizon was a thin (5 cm) layer of gray clayey subsoil. Raised-field construction apparently began with the upside-down placement of slices of topsoil plus subsoil from the surrounding area. Above

*Most of the occupation sites appear to have been abandoned 800–400 years ago, but scattered reports document the rare use of these techniques by Amerindians into colonial times (28). Early European accounts describe the practice of rain-fed agriculture by Otomac Indians in Venezuela (66) and by Tainos in Hispaniola (67), who constructed small mounds using wooden tools similar to the Arauquinoid shovel found in Suriname (37). In recent years, immigrants from Suriname (Saramaka) and from Haiti have constructed small, localized areas of raised beds in similar habitats, often in close proximity to pre-Columbian complexes. Exploiting the opportunity for comparative study of a time series, we included some of these modern analogs in our study of ecological processes.
this layer, the rest of the raised field (ca. 60 cm thick) was organic matter-rich dark soil. Much of this material must have been imported onto the raised field from further away. Transport of soil to create raised fields is suggested also by the observation in the K-VIII raised-field complex of large patches bare of topsoil, with clay-rich subsoil exposed at the surface and bearing sparse vegetation (Fig. S2). These patches are adjacent to other areas, at the same elevation and with the same subsoil, but covered with thick topsoil. Topsoil removed from these bare patches is the most likely source of the material used to create the complex of elongate raised ridges located less than 100 m away.

Raised-Field Construction and Landscape Transformation. In Savane Grand Macoua, which bears thousands of small, round mounds, data from analyses of both phytolith assemblages and carbon stable-isotope composition in soil profiles document the history of landscape transformation associated with these anthropogenically modified landscapes (Fig. S3). Profiles showed a transition from a relatively homogeneous vegetation comprised of a mixture of C4 and C3 plants, the latter including sedges (Cyperaceae), herbs (Marantaceae and Heliconia), oryzoide grasses (Poaceae: Oryzioideae) and other plants typical of frequently flooded areas, to divergence between raised fields and adjacent flooded matrix, with raised fields being dominated by C4 plants (mostly Panicoideae grasses) and the matrix continuing to show a higher contribution of C3 plants. This transition corresponds to the construction of raised fields in a previously more homogeneous landscape and the beginning of maize cultivation (see next section). In contemporary vegetation of this site, C4 species continue to be more frequent on abandoned raised fields and C3 species more frequent in the matrix (Table S2).

Plants Grown on Raised Fields and Their Production Capacity. Phytoliths of maize (Zea mays L.) (38) were detected (Fig. 3A, B, and F) in all types of raised fields from all sites examined (Piliwa, Grand Macoua, K-VIII, and Bois Diable) (Fig. S1), showing that, as in other raised-field systems in the Neotropical lowlands (e.g., 39, 40), maize was a major crop planted in these agricultural landscapes (Fig. 3 and Table S3). Phytoliths of squash (Cucurbita) also were found in one raised-field complex (Piliwa) (Fig. 3C). Finally, analysis of ceramic residues (fragments of grids used to toast food) from the Sable Blanc site yielded starch grains of maize (Fig. 3D) and manioc (Manihot esculenta Crantz) (Fig. 3E, Table S4, and SI Text).

Raised-field agriculture certainly had the capacity to support large and concentrated populations in the Guiana coast. A conservative estimate for a single annual crop, using the lowest maize productivity (2 t ha$^{-1}$) obtained from raised field experiments (5) and assuming 25% of fields in use (to allow for fallow periods, which were likely to have been necessary [41, 42]), shows that maize agricultural production would have been able to support a minimum of 234 persons in Grand Macoua (75 ha of cultivable surface) assuming a maize equivalent of 160 kg consumption per person per year, the rest of the diet being supplied by other foods (43, 44). This estimate is based on analysis of aerial photographs showing that raised-field patches cover 167 ha in Grand Macoua and that within these patches field surfaces account for ≥45% of total surface. These estimates of carrying capacity are similar to those previously proposed by Rostain (28).

Ecosystem Engineers and Self-Organizing Processes in “Fossil” Raised-Field Landscapes. Subjected to centuries of up to 4 m of highly erosive tropical rainfall each year, elevated structures presenting slopes, particularly small structures such as the abandoned raised fields in Corossony (Fig. 1), Grand Macoua (Fig. 4A), and many other sites, should have disappeared. Self-organizing mechanisms driven by ecosystem engineers can explain the persistence of raised fields many centuries after abandonment (Fig. 4). Ecosystem engineers are organisms (including ants, termites, earthworms, and plants, among others) that create, maintain, or modify physical or chemical features of habitats (32). Feedbacks generated by ecosystem engineers can drive self-organizing processes (33). In our study sites, nests of ground-dwelling social insects (principally the leaf-cutter ant Acromyrmex octospinosus, the predatory ant Eciton burchellii, and Nasutitermitinae spp. termites) are restricted entirely to abandoned raised fields (Fig. 4D, Fig. S4, and SI Text), the only parts of these landscapes not seasonally flooded (Fig. 4E). These species are widespread, and there is no reason to suspect that they have not been present continuously in these land-
scapes since long before raised fields were abandoned. These central-place foragers move materials to raised fields. *Acromyrmex* workers carry large quantities of plants to the nest to feed their fungal symbiont, and the debris from their farms is deposited on the surface in large refuse piles (Fig. 4D). Termites bring quantities of plant necromass to raised fields, where it is consumed or, together with mineral soil and fecal material, used to construct the nest (45). Organic matter brought to raised fields by these insects is incorporated into soil organic matter or mineralized by fires. Both *Acromyrmex* and *Ectatomma* construct deep nests, bringing subsoil to raised field surfaces (Fig. 4D). Transport of materials to surfaces of abandoned raised fields thus compensates at least partially for losses caused by erosion, as indicated by studies of soil movement using radionuclides (Fig. S5 and SI Text). Organic matter brought to raised fields by social insects attracts earthworms. Earthworm casts occupy virtually the entire surface of raised fields, but these biogenic structures are absent on the surface between the mounds (Fig. 4 B and C).

All these processes driven by humans and natural ecosystem engineers led to a significant (*P* < 0.05) accumulation of soil organic matter (C) as well as higher levels of total and plant-available nutrients [N, P, K (available K only) and Ca] in raised fields as compared with nearby flat reference areas without raised fields (Fig. S6A). Feedbacks driven by ecosystem engineers stabilize organic matter and nutrient accumulations in raised fields after their abandonment by human engineers. Better soil aeration and higher nutrient availability favor denser plant cover on raised fields, and woody plants (mostly *Byrsonima verrucosa* and other fire-tolerant small shrubs) are restricted almost entirely to raised fields (Fig. 4A and Table S2). Their perennial root systems and litter input further enhance soil quality on raised fields. Nevertheless, the fertility of these soils is much lower than that of other human-modified soils in Amazonia such as Amazonian Dark Earths (10).

Activities of ecosystem engineers also reduce the erodibility of raised fields. Porosity created by plant roots and by biogenic structures of engineer animals leads to nine times higher water infiltration rates in raised fields than in soils of the adjacent seasonally flooded matrix (Fig. S6B). Rainfall thus percolates into raised fields, penetrating deeply, rather than running off, and thereby reducing erosion. Greater macroaggregate stability in raised fields appears to result from higher earthworm activity, as indicated by the greater stability of aggregates in this same size class in earthworm casts (Fig. S6B).

By reducing the erodibility of raised fields and by transporting materials to them, thereby compensating erosional losses (Fig. S5 and SI Text), communities of ecosystem engineers on raised fields maintain the concentration of resources (and organisms) on raised fields and their depletion in the surrounding matrix (Fig. S6C). Such self-organizing mechanisms could have increased the resilience of raised-field agroecosystems. Experiments in contemporary rehabilitation of raised-field agriculture show declining yields after several years (41, 42); integration of fallow periods thus would have been necessary. Our results suggest that during fallow periods, self-organizing mechanisms could maintain mounds and enhance the concentration of resources within them, reducing the labor costs needed to restore raised fields in the following cultivation cycle.

Whereas ecosystem engineers maintain raised fields, they appear incapable of constructing elevated structures themselves in these environments, at least at the scale observed. None of the social insects present in these sites constructs large nest mounds. In a swath of flat terrain (4–6 m wide and 573 m long) cut through a raised-field complex by a bulldozer in the early 1980s, only small, scattered, irregular hillocks have reappeared, and engineer organisms (social insects, earthworms, and woody plants) are rare. These organisms appear incapable of producing, during a single interval between successive flooding periods, structures sufficiently elevated to escape annual obliteration of the organisms and their constructions. In these environments, the initial rapid construction of large raised fields by humans appears to have been

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Fig. 4. Raised fields and some of the ecosystem engineers that maintain them. (A) Part of the vast complex of abandoned raised fields in Savane Grand Macoua in the rainy season (April 2007). Only the abandoned raised fields are above water level. (B) Abandoned raised field in the dry season, totally covered with earthworm casts, absent from the surrounding matrix. Note higher plant density on the abandoned raised field. (C) Surface of a typical abandoned raised field, completely constituted of earthworm-produced biogenic structures. (D) Material associated with an *Acromyrmex octospinosus* nest on an abandoned raised field. Light brown material covering the top of the mound is excavated soil, yellow-brown material at center bottom is plant debris deposited from the ants’ fungal farm.
a necessary condition for the colonization of the fields by ecosystem engineers and their persistence at the scale observed here.

The landscapes produced when raised fields are abandoned (Figs. 1 and 4A) show a marked resemblance to landscapes of natural origin that exhibit regularly patterned heterogeneity (33, 46). Patterned landscapes of natural origin occur in diverse settings, from peat bogs to semiarid regions, but they all share a fundamental similarity in their ecological functioning: The regular patches are produced and maintained by scale-dependent feedbacks between organisms and their environment (33, 46). In these landscapes, resource limitation or stress strongly limits plant growth. Biological and physical mechanisms are responsible for short-distance positive feedbacks (e.g., through facilitation) and longer-distance negative feedbacks (e.g., through competition) that maintain resource concentration in some patches and resource depletion in others. Our data, from both pre-Columbian raised fields and modern analogs, show that the construction and abandonment of raised fields, followed by their colonization by natural ecosystem engineers, produced landscapes that function in the same way. Raised fields, regularly distributed patches in a seasonally flooded matrix, concentrate a crucial resource: well-drained soils. Organisms attracted by this resource also concentrate on raised fields, and their engineering activities maintain these structures and the matrix between them. Just as in self-organizing landscapes of natural origin, short-distance positive feedbacks and longer-distance negative feedbacks (e.g., greater erosion in the matrix (Fig. S5]) result in the maintenance of periodic patterns (33). This functioning could be duplicated to create a convenient experimental system for studying self-organizing processes in ecology and exploring their applications. As illustrated by artificial reefs (47), studying ecological processes initiated by abandoned human structures can inspire a rich diversity of both fundamental and applied research.

**Taphonomy of “Fossil” Raised-Field Landscapes.** To what extent are the patterns we observe today an accurate “fossil record” of patterns created by pre-Columbian people? How have these patterns been altered by postabandonment modifications? The taphonomy (48) of these “fossil” agricultural landscapes is completely unexplored. Analyzing variation in the strength of self-organizing processes provides a framework for examining how ecology can be factored into our reading of history.

Our hypothesis implies that ever since raised fields were abandoned, engineer organisms have occupied them frequently enough and have been sufficiently active to counter their erosion. This level of activity is unlikely to have existed in all of the range of environmental conditions in which raised fields were constructed. The extent to which the original morphology of abandoned raised-field landscapes is maintained and how this morphology is modified should depend on the interplay between erosion and the erosion-countering activities of engineer organisms. We observed that raised fields are not equally well conserved in all sectors within our sites. By contrast, in other sectors engineers not only conserve raised fields but add to them, building “bridges” that lead to coalescence of two or more raised fields into single, anastomosing mounds. Variation in the strength and the scale of engineer-generated positive feedbacks thus appears to cause variation in patterns, exactly as happens in periodic landscapes of natural origin (see fig. 2 in ref. 33). These dynamic landscapes thus have been truly coconstructed by the complementary actions of human and natural engineers. Their land use history has had a lasting effect on their ecology. Conversely, ecological processes that began before or after abandonment and continue today (including anthropogenic fire, long an important influence in this region) affect our reading of their history. Identifying environmental factors that influence the erosion/deposition balance is a primary focus of ongoing work.

**Implications for Interpreting the Past and Managing the Future.** Our data contribute to assessing the geographic scale of pre-Columbian human impacts within Amazonia. Some landscapes considered to be “of probable natural origin” (fig. 5.2 in ref. 11) would merit closer scrutiny in the light of our findings. Our data also have direct implications for understanding the contemporary ecological legacy of pre-Columbian agriculture. Our data indicate that, in a way unrecognized by many participants in a debate that tends to oppose the predominance of “natural” (11) or of “cultural” (12, 13) environments (but see ref. 49, pp. 71–72), important features of some present-day ecosystems are the result of interactions between cultural and natural processes. Our research shows that these opposing views can be reconciled, or at least synthesized. It also shows that studies of the resilience of pre-Columbian anthropogenic legacies need to consider the role of ecosystem engineers in the preservation of material signatures of past land use.

Understanding the complex ecological legacy of past land use is particularly important today, when debates are raging about the future of tropical forests and savannas (conversion to biofuel plantations or maintenance in a carbon economy), and when new dynamics of colonization caused by human mobility, climate change, and political conflict are playing out more intensively than at any time in human history. Our results thus may have important implications for today’s crucial goal of more sustainable use of the resources of our planet (50, 51). As in forested regions of Amazonia, there were early studies that documented the dramatic effects of biochar amendments (intentional or unintentional) by pre-Columbian farmers on the nutrient-retaining and food-producing capacities of highly weathered tropical soils (10), our findings on raised fields in seasonally flooded savannas suggest that largely forgotten pre-Columbian agricultural techniques could have useful applications today. Coupling the actions of human and natural engineers could be used to design fallows that retain resources in raised fields (Fig. S6A and B) and maintain the biodiversity of savanna environments. Exploiting mechanisms for concentrating natural resources also could help us design agroecosystems that are more resilient to human disturbance and climate change (33). Our results suggest an important dimension that must be taken into account in attempts to rehabilitate raised-field agriculture for food production today (52, 53). These experiments have shown that social, cultural, and economic factors, such as the time cost of labor input, may limit contemporary acceptability (5, 41, 42, 54) of systems whose agricultural productivity per hectare is unquestioned (see refs. 55–57 for lowland examples). Self-organizing processes in fallows could reduce the labor costs of rehabilitating fields for the next cultivation cycle. Exploiting these processes could help us design systems more appropriate to contemporary social and technological environments, thus countering a recognized barrier to the usefulness of raised-field agriculture today (5, 41, 42, 54). In these ecosystems—today considered inhospitable for agriculture—understanding and imitating how pre-Columbian farmers coupled human and natural engineering could thus point to future applications in ecological engineering.

**Materials and Methods**

We combined aerial archeology and excavations to discover, characterize, and analyze pre-Columbian sites (27, 28). Radiocarbon dates were provided by the Centre National de la Recherche Scientifique (CNRS) Center for Radiocarbon Dating (Lyon, France) and by Beta Analytic, Inc. (Miami, FL). Phytoliths and starch grains were processed, identified, and counted using standard methods and published literature (38, 58–65) and extensive reference collections at the University of Exeter and the Smithsonian Tropical Research Institute. Plant species encountered in vegetation transects on abandoned raised fields and flooded matrix were classed as possessing the C3 or the C4 photosynthetic pathway based on literature records or on the determination of δ13C values of leaf tissue. Distributions and densities of social insect nests were determined in a series of 200-m² quadrats. See SI Text for details of methods used in soil analyses and radionuclide studies.